

EARLY PLIOCENE IBISES (AVES, PLATALEIDAE) FROM SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

By

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(With 5 figures and 2 tables)

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ABSTRACT

Two species of ibises (Plataleidae) are recognized in the early Pliocene avifauna from Langebaanweg, south-western Cape Province, South Africa. One of these, *Geronticus apelex* sp. nov., is described from a partial associated skeleton and a few other referred specimens. *Geronticus apelex* was smaller than extant members of the genus and was more similar in morphology to the Palearctic species *G. eremita* than to the South African species *G. calvus*. A single end of a tibiotarsus is referred to the genus *Threskiornis* and is indistinguishable from the living species *T. aethiopicus*. These reports constitute the first Tertiary record for either genus. The living species of *Geronticus* characteristically inhabit dry, open areas and are not paludicolous. The South African species, *G. calvus*, is dependent upon short vegetation maintained by fires and grazing by ungulates for optimum foraging habitat. These ecological requirements would have been met in the early Pliocene at Langebaanweg, when the environment was becoming increasingly arid and where periodic fires and abundant ungulates are known to have been present.

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INTRODUCTION

In the extensive collections of fossil birds from the early Pliocene Varswater Formation at Langebaanweg (Rich 1980; Hendey 1981) are remains of two species of ibises (Plataleidae). The present study describes these specimens and completes the analysis of all the fossils recovered thus far from Langebaanweg that are referable to the traditional order Ciconiiformes, which, however, is an unnatural, polyphyletic assemblage (Olson 1979, 1984, 1985). Other ciconiiform families known from Langebaanweg are the Scopidae (hamerkops), with one species, *Scopus xenopus* Olson (1984), and Ciconiidae (storks), with a single new

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species of *Ciconia* (P. Haarhoff MS). Herons (Ardeidae), flamingos (Phoenicopteridae), and shoe-bills (Balaenicipitidae) are absent in these deposits, despite the fact that flamingos and herons are common in the Cape region today.

The fossils treated here are housed in the collections of the Department of Cenozoic Palaeontology at the South African Museum, Cape Town; all fossil specimen numbers are prefixed by the acronym SAM-PQ, which has been omitted below. Other museum acronyms are explained in the acknowledgements.

Comparative material examined

Skeletal material of most species of ibises is scarce. The majority of the more critical species needed for this study were represented largely or entirely by a few unsexed captive birds. The specimens examined were as follows: *Geronticus eremita* IRSB 2057, IRSB 7459, IRSB 41072, MVZ 155199; *G. calvus* TM 33348, TM 33434, TM 60076; *Pseudibis papillosa* IRSB 64593; *Bostrychia hagedash* UMMZ 158551, UMMZ 214345, USNM 322594; *B. carunculata* AMNH 3894; *Lophotibis cristata* AMNH 3788; *Threskiornis aethiopicus* USNM 558412, USNM 558413, USNM 558415, USNM 558416; *T. melanocephalus* USNM 347314; *T. spinicollis* USNM 347785; *Nipponia nippon* USNM 16687; *Mesimbrinibis cayennensis* USNM 345762, USNM 345763; *Theristicus caudatus* USNM 227359, USNM 345764; *T. branickii* USNM 10022; *Harpiprion caerulescens* USNM 227358; *Cercibis oxycerca* DMNH 58261; *Phimosus infuscatus* UMMZ 158609, UMMZ 158610, UMMZ 218530; *Eudocimus albus* USNM 19787, USNM 500882; *Plegadis falcinellus* USNM 430823, USNM 502162, USNM 502696, USNM 502698; *P. chihi* USNM 498686; *P. ridgwayi* USNM 502127; *Platalea alba* USNM 558417.

SYSTEMATICS

Family Plataleidae

Any consideration of the systematics of ibises is hampered by the lack of a modern generic revision of the family grounded in internal anatomy. In examining the skeletons of most of the extant genera of Plataleidae, it became apparent that osteological differences between genera are not particularly profound. Nor are the more distinctive characters distributed in a manner that consistently allows genera to be clustered meaningfully. Preliminary observations nevertheless suggest that departures from the generic classification of Steinbacher (1979) will eventually prove necessary. Although only a single pathological captive specimen of *Pseudibis papillosa* was available for examination, no trenchant characters by which *Pseudibis* could be separated from *Geronticus* were detected. No skeleton of the giant ibis *Thaumatibis gigantea* was available for this study; however, it would be premature to follow Holyoak (1970) in including this distinctive species in the genus *Pseudibis* without anatomical confirmation.

Genus *Geronticus* Wagler, 1832

The fossil species described below is referable to the genus *Geronticus* by the combination of (1) narrow, tapering premaxilla and mandibular symphysis, lacking an expanded tip; (2) fairly shallow, curved mandibular rami; (3) retro-articular processes of the mandible not strongly developed; (4) rostrum deep, particularly the ventral bars; (5) narrow, elongate cranium; (6) short, robust tarsometatarsi; and (7) proportionately very long wing elements.

This combination of characters is not met with in any other genus, with the possible exception of *Pseudibis*. Among African genera of ibises, *Threskiornis* and *Plegadis* have the bill markedly expanded at the tip and have much longer tarsometatarsi, particularly in *Plegadis*. *Geronticus* and *Bostrychia* are similar in sharing short tarsometatarsi and a narrow bill tip, but in *Bostrychia* the retroarticular processes of the mandible are much better developed than in the fossil species.

Geronticus apelex sp. nov.

Figs 1-5

Material

Holotype. L20692, partial associated skeleton including the following elements: 37 mm section of premaxilla including the anterior portion of the internal (ventral) narial opening; much of the cranium (partially reconstructed) including frontals, occiput, and auditory regions; portions of the mandible including 30 mm of the tip, the proximal third of the right and the left dentary, and the right articular region; half of a pterygoid; atlas; axis; right forelimb including most of the humerus (partially reconstructed), ulna lacking part of the area around the brachial depression, radius, radiale, and carpometacarpus lacking part of the minor metacarpal; right hindlimb including femur, tibiotarsus lacking distal third, and tarsometatarsus; and various small fragments, mostly cranial. The specimen is from the Quartzose Sand Member (QSM) of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

Paratypes. L13052W2, left coracoid (QSM); L28174M, scapular two-thirds of right coracoid (QSM); L4236D, scapular half of left coracoid (Pelletal Phosphorite Member (PPM), bed 3aS); L20755K, left scapula lacking posterior fourth (QSM). Including the holotype, the minimum number of individuals is two.

Measurements of holotype (in mm)

Cranium: width at point of articulation of nasal bars, 16,8; width through auditory region, 23,3; estimated length from point of articulation of nasal bar to posterior margin of occiput, 44. Mandible: length as reconstructed, 150; width at a point 20 mm caudad from tip, 3,2; antero-posterior diameter of articular surface, 7,0; medio-lateral diameter of articular surface, 8,0; least depth through articulation, 6,7. Atlas: depth, 7,4. Axis: width, 11,3. Humerus: length, 111,4;



Fig. 1. Right lateral view of skulls and mandibles of *Geronticus*. A. *G. apelex* sp. nov., holotype, SAM-PQ-L20692. B. *G. eremita*, MVZ 155199. C. *G. calvus*, TM 33348. The occipital crest in *G. eremita* may be better developed in presumably older individuals but never approaches the condition in *G. calvus*. Scale is in mm.

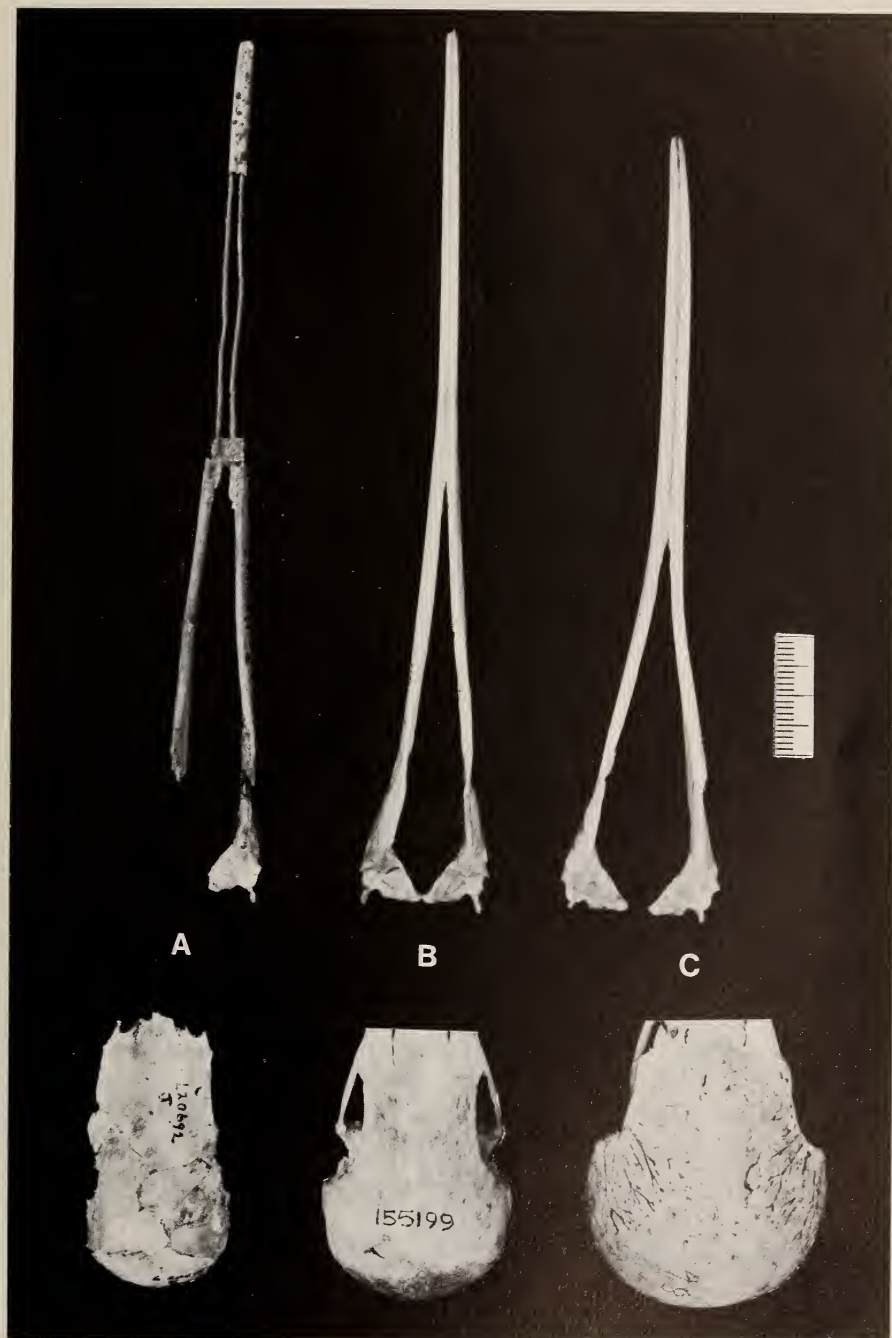


Fig. 2. Dorsal view of mandibles (top row) and crania (bottom row) of *Geronticus*.
 A. *G. apex* sp. nov., holotype, SAM-PQ-L20692. B. *G. eremita*, MVZ 155199.
 C. *G. calvus*, TM 33348. The cranium of *G. apex* is partly reconstructed and is lacking portions along the lateral margins that would make it slightly wider. Scale is in mm.

shaft width at narrowest point, 8,4; shaft width at proximal limit of brachial impression, 12,4; greatest diameter of brachial impression, 9,0; distal width, approximately 18,5; length of dorsal condyle, 7,6. Ulna: length, 122,5; proximal width and depth, $13,3 \times 9,0$; width and depth of shaft at midpoint, $5,5 \times 6,1$; distal width and depth, $7,8 \times 9,7$. Radius: length, 116,4; greatest proximal diameter, 6,7; least and greatest diameter of shaft at midpoint, $3,2 \times 4,6$; greatest distal diameter, 8,9. Carpometacarpus: length, 60,8; depth through alular metacarpal, 13,4; proximal width through trochleae, 6,0; width and depth of major metacarpal at midpoint, $5,0 \times 3,9$; greatest distal diameter, 9,2. Femur: length, 57,4; proximal width, 12,5; depth of head, 5,2; width and depth of shaft at midpoint, $5,5 \times 4,9$; distal width, 12,7; depth through medial condyle, 8,8; depth through lateral condyle, 10,3. Tibiotarsus: proximal width through articulation, 10,1; length of fibular crest, 17,1; width and depth of shaft at approximate midpoint, $5,2 \times 4,3$. Tarsometatarsus: length, 64,6; proximal width, 11,6; depth through hypotarsus, 10,9; width and depth of shaft at midpoint, $4,9 \times 3,8$; distal width, 11,7; width and depth of middle trochlea, $4,5 \times 5,9$.

TABLE 1

Length measurements (mm) of major elements of *Geronticus apelex* sp. nov. compared with extant species of *Geronticus* and *Pseudibis* (means in parentheses).

	<i>G. apelex</i> (n = 1)	<i>G. eremita</i> (n = 4)	<i>G. calvus</i> (n = 3)	<i>P. papillosa</i> (n = 1)
Coracoid	40,4	45,4–47,2 (46,1)	45,7–47,0 (46,1)	—
Humerus	111,4	126,3–130,0 (128,6)	117,6–124,1 (119,9)	—
Ulna	122,5	139,6–145,3 (142,5)	128,0–137,5 (131,8)	138,9
Carpometacarpus	60,8	71,0–72,9 (71,9)	64,4–69,8 (66,8)	71,5
Femur	57,4	64,8–66,7 (65,8)	65,5–69,9 (67,2)	64,7
Tarsometatarsus	64,6	72,9–74,6 (73,7)	69,1–77,2 (72,2)	81,5

Measurements of paratypes (in mm)

Coracoid, L13052W2: length from head to medial angle of sternal articulation, 40,4; length and width of glenoid facet, $10,3 \times 5,8$. Coracoid, L28174M: length and width of glenoid facet, $10,5 \times 6,3$. Coracoid, L24236D: length and width of glenoid facet, $10,8 \times 6,2$. Scapula, L20755K: greatest diameter of anterior end, 9,7.

Diagnosis

Smaller than either of the extant species of *Geronticus* (or *Pseudibis*) (Table 1). Cranium rather narrow and elongate, lacking any of the occipital expansion into a crest as seen in the two living forms (greatly exaggerated in *G. calvus*, in which the top of the cranium is monstrously inflated both laterally



Fig. 3. Wing elements of *Geronticus apex* sp. nov., holotype, SAM-PQ-L20692 (on left in each pair) and *G. eremita*, MVZ 155199. A. Humeri. B. Ulnae. C. Carpometacarpi. Scale is in mm.

and posteriorly). Mandibular symphysis narrow as in *G. eremita*, not broader and more flattened as in *G. calvus*. Compared to modern species of *Geronticus*, the procoracoid foramen of the coracoid is smaller, the brachial depression of the humerus is smaller, not extending as far proximally, with the brachial depression of the ulna being correspondingly small; the trochanter of the femur in lateral view is more proximally extended into a point, appearing narrower and less truncate. The wing elements are proportionately longer than in *G. calvus*, being more similar to those of *G. eremita*.



Fig. 4. Hindlimb elements of *Geronticus apelex* sp. nov., holotype, SAM-PQ-L20692 (on left in each pair) and *G. eremita*, MVZ 155199. A. Femora. B. Tibiotarsi. C. Tarsometatarsi. Scale is in mm.

As mentioned above, *Pseudibis* is very similar to, and possibly congeneric with, *Geronticus*. In the one poor skeleton of *P. papillosa* examined, the distal foramen of the tarsometatarsus was more proximally situated than in *G. apelex* or in any of the modern specimens of *Geronticus*.

Distribution

Early Pliocene Varswater Formation (Quartzose Sand Member and Pelletal Phosphorite Member bed 3aN) at Langebaanweg, south-western Cape Province, South Africa.

Etymology

Greek, *a-*, without, and *pelex*, helmet, in reference to the lack of an expanded bony occipital crest such as found in modern species of *Geronticus*. The name is a feminine noun in apposition.

Remarks

The specimens of *Geronticus apelex* provide the only Tertiary record for the genus.

The paratypical coracoids and scapula agree with a species the size of the holotype of *G. apelex*. The referred coracoids differ from *Plegadis* in having the sternal articulation convex rather than concave, from *Threskiornis* in not having the area of muscular attachment on the dorso-sternal surface markedly excavated, and from *Platalea* in lacking the distinct, wide, flat clavicular articulation. The coracoids are distinctive in having the procoracoid process expanded posteriorly and medially, giving the shaft a very robust appearance. In this respect the coracoids also differ from *Plegadis* and *Threskiornis* and more closely resemble *Geronticus* and *Bostrychia*. However, there appears to be considerable intra- and interspecific variation in the development of the procoracoid process in *Geronticus* and *Bostrychia*.

The wing elements seem disproportionately long in the holotype of *Geronticus apelex* and this is confirmed by computing the ratio of the length of the long bones to femur length (Table 2). Dividing by the length of the most

TABLE 2

Ratios of lengths of some long bones of African ibises divided by femur length. All ratios for *Geronticus apelex* are computed from the holotype. Except for one male of *G. eremita*, all the specimens of *Geronticus* and *Bostrychia* were unsexed. In *Threskiornis* and *Plegadis*, measurements are for two males and two females each; in *Plegadis* there is considerable sexual dimorphism in the size of the tarsometatarsus, which is proportionately much longer in males.

	Humerus	Ulna	Carpometacarpus	Tarsometatarsus
<i>Geronticus apelex</i> sp. nov. (n = 1)	1,94	2,13	1,06	1,12
<i>Geronticus eremita</i> (n = 4)	1,93-1,98	2,14-2,22	1,07-1,11	1,10-1,14
<i>Geronticus calvus</i> (n = 3)	1,77-1,80	1,93-1,98	0,97-1,01	1,05-1,10
<i>Bostrychia hagedash</i> (n = 3)	1,78-1,82	2,05-2,10	0,99-1,02	1,11-1,24
<i>Bostrychia carunculata</i> (n = 1)	1,79	2,05	0,98	1,04
<i>Threskiornis aethiopicus</i> (n = 4)	1,66-1,69	1,91-1,95	0,94-0,97	1,33-1,41
<i>Plegadis falcinellus</i> (n = 4)	1,59-1,68	1,69-1,91	0,95-0,99	1,52-1,78

complete paratypical coracoid yielded practically identical results. By either standard, *G. apelex* has a relatively longer humerus, ulna, and carpometacarpus than any of the species compared except *G. eremita*. The relative shortness of the tarsometatarsus in *Geronticus*, as compared to *Threskiornis* and *Plegadis*, is also demonstrated.

The greater similarity in the proportions of the wing of *G. apelex* to those of *G. eremita*, as opposed to *G. calvus*, may reflect migratory or nomadic propensities in the fossil species. *G. eremita* migrates well out of its breeding area in the autumn and early winter, whereas *G. calvus* is more sedentary. In lacking the great occipital expansion of *G. calvus*, the fossil species is likewise more similar to *G. eremita*, in which the occipital crest is much less developed. Within *Geronticus*, the lack of an expanded occipital crest would almost certainly be primitive, as such a crest occurs nowhere else in the family. The narrower and less flattened mandible of *G. apelex* is also more similar to that of *G. eremita* than *G. calvus*.

The ranges of *G. eremita* and *G. calvus* are now widely separated, with the former having occurred historically in Europe, the Middle East, and in northern Africa, although it is now reduced to two breeding populations, one in Turkey and the other in Morocco (Smith 1970). *Geronticus calvus* is restricted to South Africa, being found in mountainous areas from southern Transvaal to north-eastern Cape Province, having formerly extended to the south-western Cape (Siegfried 1966). The two species of *Geronticus* are now commonly regarded as forming a 'superspecies' (e.g. Snow 1978). The superspecies concept has become

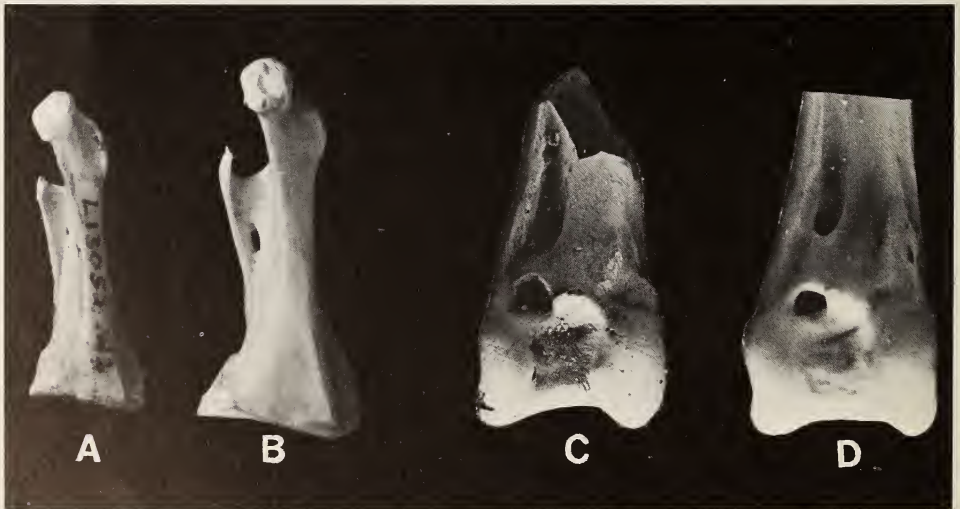


Fig. 5. Left coracoids of *Geronticus* (A-B) and distal ends of left tibiotarsi of *Threskiornis* (C-D). A. *G. apelex*, sp. nov., paratype, SAM-PQ-L13052W2. B. *G. calvus*, TM 33434. C. *T. aff. aethiopicus*, SAM-PQ-L28479G. D. *T. aethiopicus*, USNM 558413.

A and B, natural size; C and D, twice natural size.

very fashionable in recent years but through constant abuse and misapplication (e.g. American Ornithologists' Union 1983) has lost whatever utility it may once have had. In the case of *Geronticus*, it is doubtful that the superspecies category is appropriate. The differences between the two living species, at least in skull morphology, are considerable and it is possible that their ancestors may have existed sympatrically, particularly if one of them were smaller in size, as is *G. apelex*. The great differences in cranial adornment may perhaps have evolved as specific isolating mechanisms at a time when the two species were formerly in contact. Taking this view, *G. apelex* could be regarded as a smaller ancestral form of *G. eremita*, to which it is most similar.

With the available evidence, however, there is no satisfactory basis for deciding whether *G. apelex* represents (a) an extinct lineage that was contemporary with the ancestors of *G. eremita* and *G. calvus* and that left no descendants, (b) the primitive direct ancestor of one or the other of the two living species, or (c) the primitive sister group of both *G. eremita* and *G. calvus* that gave rise to both forms subsequently. The last seems the least likely, however, in view of the geologically young age of the Langebaanweg deposits and of the fact that modern species lineages were already clearly established in other groups of birds in the same deposits.

Genus *Threskiornis* Gray, 1842

Threskiornis aff. *aethiopicus* (Latham, 1790)

Fig. 5C

Material

Distal end of left tibiotarsus L28479G.

Distribution

Early Pliocene Varswater Formation (QSM) at Langebaanweg, southwestern Cape Province, South Africa.

Measurements

The distal width of this specimen is 13,1 mm, which is very near the mean for this measurement in the living species *Threskiornis aethiopicus* (12,1–14,4 mm, mean 13,2 mm, n = 8).

Remarks

This specimen is larger than in modern African species of ibises except *T. aethiopicus*, and differs further from *Geronticus* and *Bostrychia* in the much more prominent tubercle above the intercondylar fossa, this being almost lacking in *Geronticus* and only slightly better developed in *Bostrychia*. It is much too large and robust for *Plegadis*. Compared to *Platalea* it is relatively stouter, the intercondylar fossa is shallower and wider, and the distal end in distal view is not

nearly as elongated antero-posteriorly. This specimen cannot be distinguished from *T. aethiopicus*. It provides the only Tertiary record for the genus *Threskiornis*.

DISCUSSION

Although ibises are usually considered to be closely associated with marshes and fresh water, the modern relatives of the two species found in the Langebaanweg deposits are not restricted to such habitats. In fact, *Geronticus apelex* probably indicates quite different conditions, because both the modern species of *Geronticus* characteristically inhabit open, arid areas or grasslands. Both are also gregarious and nest in regions with rocky escarpments. Such outcrops occur in the Piketberg massif, some 50 km from Langebaanweg. Because *G. apelex* may have been migratory or nomadic, it need not have bred close to the site of deposition.

The living species *Geronticus eremita* is found 'most often on dry wadi beds, rocky slopes or semi-desert' (Cramp 1977: 344). *Geronticus calvus* frequents open grasslands and forages extensively in burnt areas, resorting to heavily grazed grasslands and pastures outside of the burning season (Manry 1981, 1985a, 1985b). Before the onset of human disturbance, Manry (1981) considered that suitable habitat for *G. calvus* would have been maintained by lightning-caused fires and grazing by native ungulates, particularly the black wildebeest, *Connochaetes gnou*.

The habitat requirements of *Geronticus* in general, and of *G. calvus* in particular, fit very well with the palaeoecological conditions inferred at the time of deposition of the Varswater Formation at Langebaanweg, when the environment was becoming drier and cooler and the vegetation was giving way to open grassland and fynbos (Hendey 1981). There is considerable evidence not only for the presence of numerous ungulates but for the existence of lightning-caused fires as well (Hendey 1981). Thus, the ecological conditions at Langebaanweg in the early Pliocene would seem to have been ideal for a species of *Geronticus*.

Threskiornis aethiopicus is usually associated with water, particularly areas of fresh-water marsh, which may be a prerequisite for breeding. However, in the Cape region today it is also found along the coast and is commonly seen foraging in open, arid pasturelands far from any body of water (McLachlan & Liversidge 1978), for which reason little palaeoecological significance attaches to the presence of a single individual of *Threskiornis* in the Langebaanweg deposits.

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